

## Allocating time between feeding, resting and moving by the two-spotted spider mite, *Tetranychus urticae* and its predator *Phytoseiulus persimilis*

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### ABSTRACT

This study characterizes the timing of feeding, moving and resting for the two-spotted spider mite, *Tetranychus urticae* Koch and a phytoseiid predator, *Phytoseiulus persimilis* Athias-Henriot. Feeding is the interaction between *T. urticae* and plants, and between *P. persimilis* and *T. urticae*. Movement plays a key role in locating new food resources. Both activities are closely related to survival and reproduction. We measured the time allocated to these behaviours at four ages of the spider mite (juveniles, adult females immediately after moult and adult females 1 and 3 days after moult) and two ages of the predatory mite (juveniles and adult females). We also examined the effect of previous spider mite-inflicted leaf damage on the spider mite behaviour. Juveniles of both the spider mite and the predatory mite moved around less than their adult counterparts. Newly emerged adult female spider mites spent most of their time moving, stopping only to feed. This represents the teneral phase, during which adult female spider mites are most likely to disperse. With the exception of this age group, spider mites moved more and fed less on previously damaged than on clean leaves. Because of this, the spider mite behaviour was initially more variable on damaged leaves. *Phytoseiulus persimilis* rested at all stages for a much larger percentage of the time and spent less time feeding than did *T. urticae*; the predators invariably rested in close proximity to the prey. Compared to adult predators, juveniles spent approximately four times as long handling a prey egg. The predator–prey interaction is dependent upon the local movement of both the predators and prey. These details of individual behaviours in a multispecies environment can provide an understanding of population dynamics.

**Key words:** Behaviour, trophic interactions.

### INTRODUCTION

The two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), is a serious pest on over 30 economically important crops, including corn, cotton, cucumbers, peanuts, sorghum, beans, melons, strawberries and a variety of greenhouse ornamentals. Foliar damage occurs because mites remove the

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chlorophyll, water and nutrients from leaf cells (van der Geest, 1985). Feeding is usually localized; spider mites deposit eggs close to where they feed and most offspring do not move very far from where they hatch. In this way clusters or patches of spider mite-infested leaves develop. Spider mites respond to this localized feeding-induced leaf damage by dispersing away from damaged leaves (Suski and Naegele 1968; Kondo and Takafuji, 1985; Li and Margolies, 1993). Because of their ability to disperse and the explosive growth potential of mite populations (Sabelis, 1981), mites can infest and kill entire plants.

Predatory mites have been used successfully to control spider mites in greenhouses, in orchards, in vineyards and on strawberries. One commonly used predator, *Phytoseiulus persimilis* Athias-Henriot, is a specialist on spider mites. Adult females show a type II functional response (Eveleigh and Chant, 1981a; Sabelis, 1990); the per capita consumption is limited by their gut absorption rate (Eveleigh and Chant, 1981b; Sabelis, 1981). Therefore, at higher prey densities, the ability of a predator population to limit spider mite populations may depend more on the number of predators that aggregate in a prey patch than on individual predators' functional responses (Eveleigh and Chant, 1982a). *Phytoseiulus persimilis* exhibits area-restricted searching behaviour in response to the prey density (Eveleigh and Chant, 1982b), which leads to strong aggregation on leaflets and leaves (Zhang and Sanderson, 1993). In the presence of prey and prey-related cues (e.g. webbing), *P. persimilis* reduce their walking speed and increase the length of their stops (Hislop and Prokopy, 1981).

During the time a predator is in a prey patch, the former alternately searches for and consumes prey, rests and oviposits. However, our knowledge concerning the timing of movement and feeding by both mite species is limited. The timing of mite behaviours will show how mites allocate their time relevant to the tritrophic interaction of the plant, herbivore and predator. Characterization of individual activities gives valuable information about the limitations of these interactions. Details of individual behaviours in a multispecies environment can provide an understanding of population dynamics in larger systems (Bernstein *et al.*, 1988; Werner, 1992). This study characterizes the timing of the feeding, moving and resting behaviours of *T. urticae* and *P. persimilis*. The feeding behaviour is the interaction between *T. urticae* and plants and between *P. persimilis* and *T. urticae*. Movement behaviour also plays a key role in locating new food resources. These behaviours are compared, on healthy and spider mite-damaged leaves, between immature and adult female spider mites and immature and adult *P. persimilis*.

## MATERIALS AND METHODS

### *General methods*

Experiments were conducted from May 1993 to May 1994. The mite colonies and all experiments used 'bush baby' variety lima beans, *Phaseolus lunatus* L., as

the host plant. Experiments were performed with a *T. urticae* laboratory colony obtained from North Carolina in September 1990 and kept on lima bean in a 16:8 (L:D) photoperiod. The colony was infused with more *T. urticae* obtained from a garden in Manhattan, KS in June 1992. *Tetranychus urticae* were reared on 0.3 × 0.6 m flats containing approximately 60 bean seedlings each and the flats of the seedlings were changed weekly.

The *P. persimilis* colony was started with approximately 2000 mites from Rincon-Vitova Insectaries Inc. (Ventura, CA) in April 1993. *Phytoseiulus persimilis* were reared in a separate rearing room from *T. urticae* colonies. Predators were kept on spider mite-infested lima bean leaves in a plastic chamber with a fine mesh lid and an open bottom. The box itself was placed within a tub of water, which served as a barrier to predator escape or infestation from the outside. A wire mesh platform was placed in the container, so that spider mite-infested lima bean seedlings could be supported with their roots in the water. Spider mite-infested seedlings were added to the colony twice a week. The rearing room was kept between 25 and 30°C with a 17L:7D photoperiod. The relative humidity fluctuated between 20 and 70%.

The behaviour of individual mites was observed on 30 cm<sup>2</sup> discs cut from bean leaves. For each mite observed a freshly cut leaf disc was floated, bottom-side up, in a Petri dish filled with water; this kept the disc from drying out too quickly and inhibited mite emigration from the leaf disc. Experiments were conducted at 24 ± 2°C and 20–50% relative humidity in the room. However, the relative humidity on the leaf surface was probably above 70% (Willmer, 1982). Light during the experiments was provided by 40 W cool-white fluorescent lights suspended approximately 2 m above the work surface, augmented by natural sunlight from nearby windows. We observed each mite tested individually. Although we did not find any difference in the mite behaviour between tests conducted in the morning and those in the afternoon (personal observation), most observations of the mite behaviour were made in the afternoon for consistency. We used a dissecting scope to observe the mite behaviour continuously during the observation period.

#### *Spider mite activity*

We examined both the juvenile and adult female behaviour. For the juveniles, 30 immature *T. urticae* (approximately 10 larvae and 20 proto- and deutonymphs) were observed for 1 h on clean leaf discs. Immature mites were taken from the leaves of the colony and placed on the test leaflet for 15 min prior to the trial observations. It was difficult to discern between feeding and non-feeding reliably in non-moving immature mites. Therefore, immature mites were described as either moving or stationary.

Twenty-seven adult female *T. urticae* (nine newly emerged, nine 1 day old and nine 3 days old) were each observed for 1 h. Adult females of known age were obtained by collecting quiescent deutonymphs (QDs), the last immature stage,

which were guarding males from the colony and placing them on a leaf disc. Because mating occurs immediately after adult female moult, newly emerged adult females were ready to be tested the next day. A female was kept on the leaf for up to 3 days for trials with older mites. A test mite was placed in a Petri dish arena 15 min prior to the start of observation; this time was found to be adequate for the mite to settle from its startle response. We recorded the starting time and duration of each of three behaviours: feeding, moving and resting. Feeding was differentiated from 'resting' (i.e. sitting still) by (1) the orientation of the palps in relation to the leaf surface (towards when feeding) and (2) the movement of fluids seen through the cuticle of the mite (active pumping when it was feeding). Oviposition was recorded as a point event without duration. The total time moving and total time spent stationary were also compared between the adult and immature *T. urticae*, with adult stationary behaviour defined by summing the feeding and resting time.

#### *Influence of leaf damage on spider mite activity*

The leaf condition is a major factor affecting various forms of spider mite dispersal (Bernstein, 1984; Margolies and Kennedy, 1984). These experiments measured individual spider mite behavioural reactions to a leaf with a moderate amount of spider mite-inflicted feeding damage. We collected nine adult female mites immediately after they moulted (hereafter referred to as newly emerged), nine at 1 day after moult, and nine at 3 days after moult; we also collected 30 immature mites as described previously. In these trials, a healthy growing leaf was infested with 20 adult female *T. urticae* which were allowed to feed for 2 days. Tanglefoot around the petiole inhibited spider mite emigration and resulted in a consistent feeding damage of 40 mite days (20 mites  $\times$  2 days). The leaves showed moderate stippling from feeding by the mites. The damaged leaf was then cut from the petiole and placed on wet cotton upside down in a Petri dish. The 20 resident adult females were removed carefully to leave the *T. urticae* silken webbing and eggs intact. A new spider mite was transferred to a damaged leaf, allowed to acclimatize for 15 min and then observed for 1 h as above. We compared the behaviours on clean and damaged leaves for the juvenile and three adult age groups.

#### *Predatory mite activity*

On leaves without prey, predators quickly began edge walking and moved almost constantly; they rarely stayed on a leaf for the entire observation period (1 h) and usually attempted to walk over the wet cotton on which the leaf was placed, in which they became stuck. Because of this, we only measured the predator behaviour on spider mite-infested leaves. Eighteen immature and 18 adult female predators were observed. A *P. persimilis* immature or adult female was transferred from a Petri dish with ample prey to a spider mite-infested leaf in

a Petri dish arena. Based on preliminary observations, we allowed 60 min for the predator to acclimatize to the arena before recording data. The predator was observed continuously for 1 h and moving, feeding and resting bouts were recorded.

### Analysis

An IBM PC computer running Observer<sup>TM</sup> software was used to record the behaviours. Statistical analysis was performed with the SAS Institute, (1992) program using the mixed procedure with repeated measures. This procedure was used to describe the repeated measurements on each mite. Each trial yielded a frequency (number of occurrences per hour), a mean behaviour bout length (in seconds) and a total time for each of the recorded behaviours. Least-squares analysis was performed for the differences between the mite ages based on the behaviours. For example, the total feeding time for each newly emerged adult mite was summed from individual bouts and a mean was calculated. This was compared with the mean total feeding time for 3 day old mites to determine whether the proportion of the total time feeding was different. Comparing the mean length of feeding bouts between mites of different ages would indicate whether mites tend to feed for similar time periods in each bout. The mean frequency of the feeding events was also compared between adult age groups to determine whether mites of different ages have different feeding bout frequencies. Similar tests were performed for moving and resting for all ages.

Four types of analyses are given based on the hour-long trial data from adult *T. urticae*. The leaf damage trials are included in this analysis. This grouping facilitates the comparison of behaviour on clean, undamaged leaves versus previously infested, damaged leaves. All probability values given are from the three-way interaction term of behaviour-age-damage in least-squares means analysis unless otherwise noted.

We used the sequence of the behaviour of each individual to calculate the overall frequencies of transitions from a given behaviour to all other behaviours that could follow it. The transition probabilities between behaviours and the indices of the variability of those transitions were calculated for each damage level and age. The variability of behavioural transitions between behaviours is described by the stereotypy index ( $SI = \Sigma(P_{ij})^2 - (\Sigma P_{ij})^2 / (2/(0.5)^{1/2})$ ) (Haynes and Birch, 1984).  $P_{ij}$  is the probability of transition from behaviour ( $i$ ) to behaviour ( $j$ ). The transition probabilities and stereotypy were calculated based on 57 *T. urticae* making 830 transitions and 36 *P. persimilis* making 284 transitions. A weighted mean SI value was calculated for each treatment group of individuals; this mean was weighted with the number of transitions from the behaviour. An index value near zero indicates that the transitions were evenly distributed between all the possible succeeding behaviours. A value near one indicates that the transition was usually to one succeeding behaviour. Haynes and Birch (1984) stated that the SI provides an objective, quantitative measure of the fixity of a behavioural sequence in a population. A  $\chi^2$  analysis was performed on

the behavioural transition matrices to test for differences in the stereotypy values between ages and damage levels.

## RESULTS AND DISCUSSION

The behaviours of both the juvenile and adult spider mites were affected by previous spider mite feeding damage. Although juvenile *T. urticae* spent more time stationary than moving ( $p < 0.001$ ) regardless of leaf damage (Fig. 1c), they had longer moving bouts (Fig. 1a) and spent more total time moving (Fig. 1c) on damaged than on clean leaves ( $p = 0.0106$  and  $p = 0.0255$ , respectively). Juvenile spider mites moved more and probably fed less on damaged leaves because they encountered more depleted leaf tissue. Spider mites on previously feeding-damaged leaves may not be able to obtain enough food and water, which can increase walking (Suski and Naegele, 1968). This situation is common because of the clustered feeding and oviposition of the adults and the relatively poor dispersal ability of the juveniles. The time spent moving undoubtedly resulted in a higher energetic cost than remaining stationary and also represents lost feeding time. The result is probably detrimental to their development, which may help explain why a moderate intraspecific density increases the development time and mortality of immature *T. urticae* (van Impe, 1984).

Unlike the juveniles, newly emerged adult female *T. urticae* spent most of their time moving rather than feeding or resting ( $p = 0.007$  and  $p = 0.0286$ , respectively), regardless of leaf damage (Fig. 4). This age represents the teneral phase, during which adult female spider mites are most likely to disperse (Hussey and Parr, 1963; Li and Margolies, 1993). The feeding bouts immediately after moult were of similar duration on damaged and clean leaves during this time, averaging approximately 300 s (Fig. 2a). This bout length compares with approximately 400 s as reported by Kolmes *et al.* (1991). Feeding occurred with a similar frequency on the damaged and clean leaves (Fig. 3a) and, hence, the total feeding time was similar (Fig. 4a). The newly emerged adult guts are empty and the first hours of feeding may be a period of refuelling. However, mites on clean leaves were either probing the leaf or feeding; they rarely rested (Fig. 3c).

As the adults became older, the allocation of time on damaged and clean leaves reflected the same trends exhibited in the juveniles. The feeding bouts decreased on both the clean and damaged leaves (Fig. 2a); the frequency of feeding increased on both as well, but not to the same extent on the two types of leaves (Fig. 3a). By 1 day after moulting, the adult mites fed more frequently on clean than on damaged leaves ( $p < 0.0108$ ), which resulted in their spending more total time feeding on clean leaves (Fig. 4a). On clean leaves moving bouts also became progressively shorter, but did not change on damaged leaves (Fig. 3b). Although the mites also moved more frequently on clean leaves ( $p = 0.0052$ ), they rested less frequently than on damaged leaves (Fig. 3c). The result was that the older adult mites spent a larger percentage of their time feeding (Fig. 4a), and less time moving (Fig. 4b) on clean leaves than on damaged ones. Because adult female

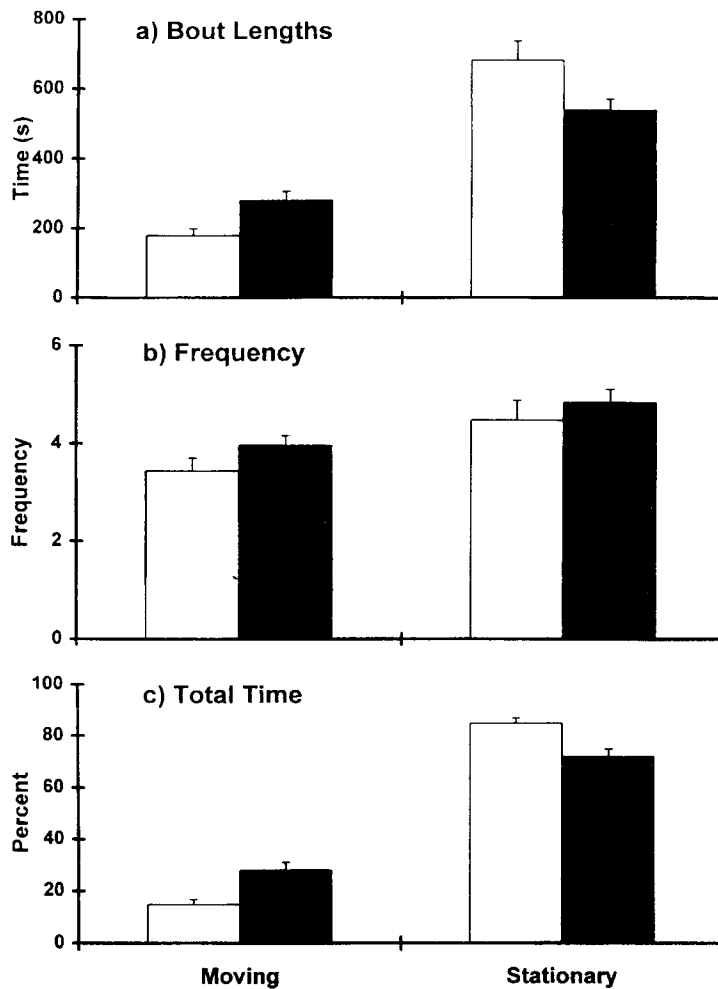


Fig. 1. (a) Bout length, (b) frequency of occurrence and (c) percent of total time of immature *T. urticae* on clean (open bars) and feeding-damaged (solid bars) leaf discs.

mites continued to spend approximately half their time moving on damaged leaves, while on clean leaves they spent more time feeding than moving ( $p = 0.0053$ ), we might expect to see dispersal from poor feeding sites and settling into better ones (Suski and Naegele, 1968). Interestingly, the presence of predators may have a similar effect as poor food quality, that is spider mites may spend less of their time feeding and more time moving when *P. persimilis* is present than when the predator is absent (A. Janssen, personal communication).

Initially, the transitions were much more variable (i.e. less stereotypical) on the damaged leaves than on the clean ones. However, the stereotypy index on the

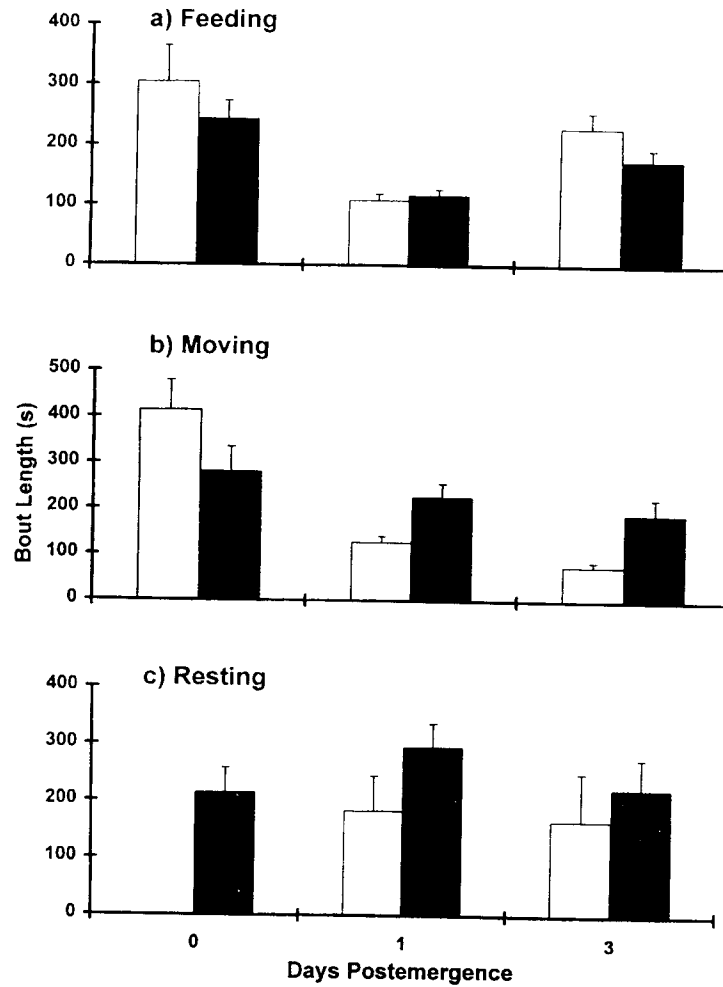


Fig. 2. Bout lengths for (a) feeding, (b) moving, and (c) resting by adult female *T. urticae* at three ages on clean (open bars) and feeding-damaged (solid bars) leaf discs.

damaged leaves increased to similar levels as the mites became older. As the mites aged, particularly on clean leaves, the females quickly settled into the egg laying phase, which should continue for the rest of their lives. By examining seven replicates in which oviposition had occurred, the mean time needed to oviposit was calculated to be  $660 \pm 97$  s (mean  $\pm$  SD), based on the length of time of the resting bout during which an egg was laid. Egg deposition took approximately 1 min. On clean leaves, the adults often spent several minutes webbing near the leaf midrib before settling to oviposit. *Tetranychus urticae*, particularly the young adults, rested more on the damaged leaves than on clean

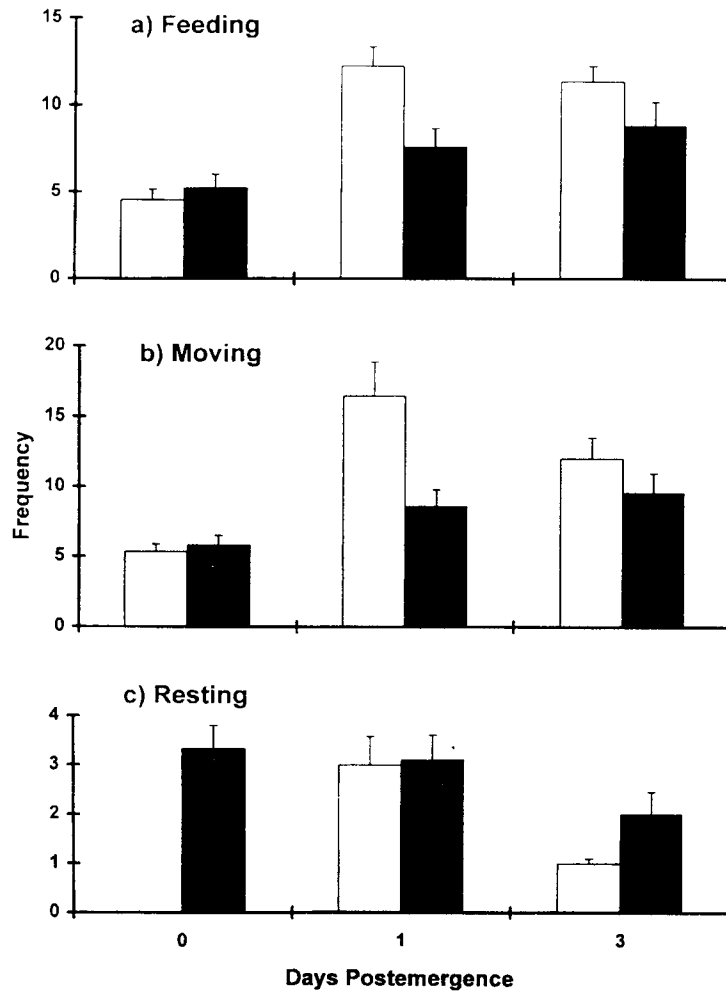


Fig. 3. Frequency of occurrence of (a) feeding, (b) moving and (c) resting by adult female *T. urticae* at three ages on clean (open bars) and feeding-damaged (solid bars) leaf discs.

ones. It may have been that, when faced with inadequate resources, resting saved internal reserves. An increased resting time represents slowed catabolism and loss of feeding time, both of which reduce egg production. This may explain why a high intraspecific density reduces fecundity (Davis, 1952) and starvation delays oviposition (Krainaker and Carey, 1990).

Like immature *T. urticae*, immature *P. persimilis* moved less than predator adults ( $p=0.0115$ ). *Phytoseiulus persimilis* juveniles spent more time resting than feeding or moving ( $p=0.0077$  and  $p=0.0043$ , respectively), whereas the adult female predators spent more time moving or resting than feeding

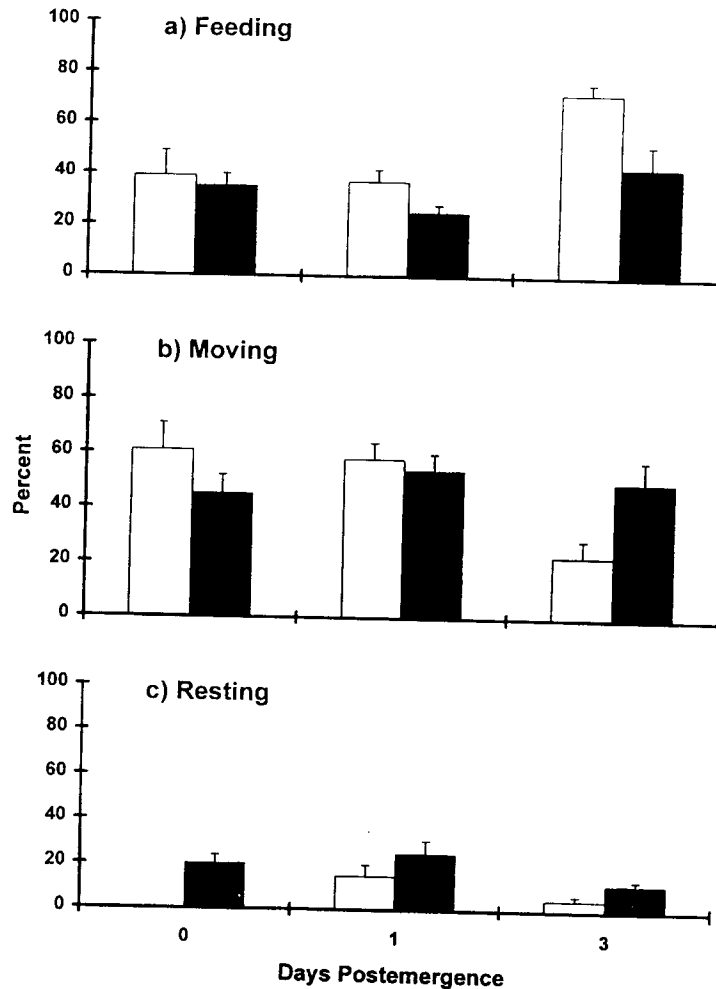


Fig. 4. Percent of total time spent (a) feeding, (b) moving and (c) resting by adult female *T. urticae* at three ages on clean (open bars) and feeding-damaged (solid bars) leaf discs.

( $p < 0.0001$  and  $p < 0.0001$ , respectively). Immature *P. persimilis* had more fixed transitions than adults (Fig. 6) because the former fed less often (Fig. 5b); immature predators fed only four times compared to the 20 observations for adults. Individual bouts of feeding and resting (Fig. 5a) were shorter for adult *P. persimilis* than for juveniles ( $p < 0.0001$  and  $p = 0.0252$ , respectively); compared with adult female predators, juvenile predators spent approximately four times as long with each prey egg. The total adult feeding time was also less ( $p = 0.0001$ ). The adult predators showed more fixed behaviour in transitions from feeding ( $p = 0.0221$ ). In general, the stereotypy indices were considerably

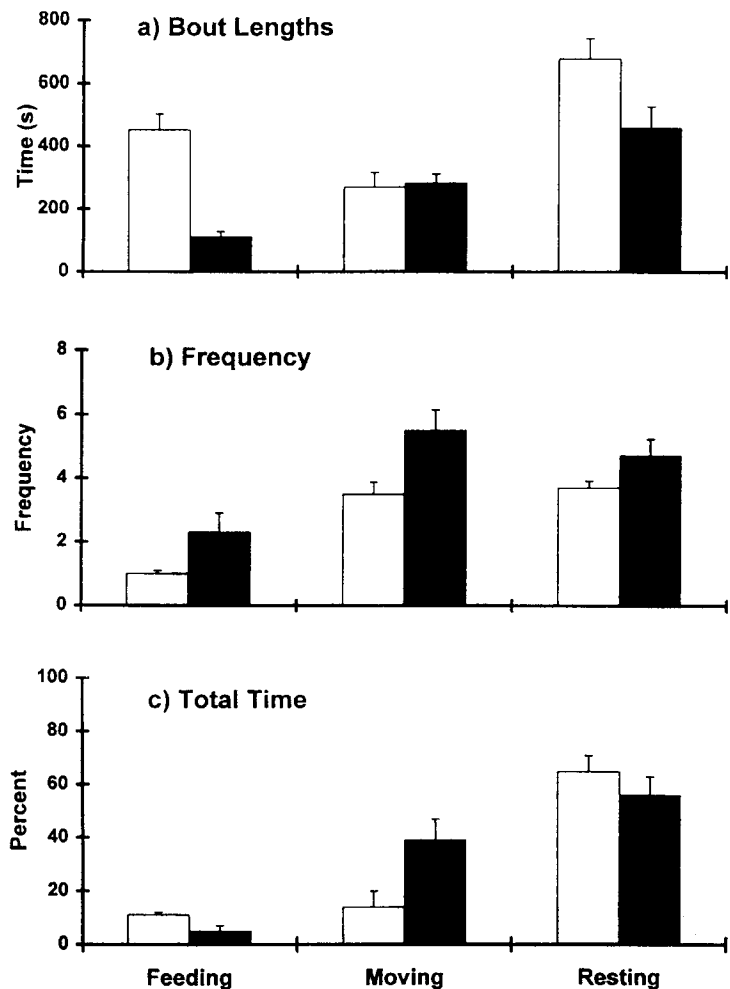


Fig. 5. (a) Bout length, (b) frequency and (c) percent of total time of feeding, moving and resting by immature (open bars) and adult (solid bars) *P. persimilis*. All trials were run on spider mite-infested leaf discs.

lower for the adults because of their higher frequency of feeding, which interrupts the resting and moving transitions.

*Phytoseiulus persimilis* rested at all stages for a much larger percentage of the time and spent less time feeding than did *T. urticae*. The adult predators rested more frequently than the immature predators ( $p = 0.0239$ ). Resting invariably occurred in close proximity to prey and usually in the most densely webbed area of the leaf arena. During the resting time some metabolic activity occurred. The limited ability to disperse and the lower food requirements of juveniles relative to

## Behavioral Transitions and Stereotypy

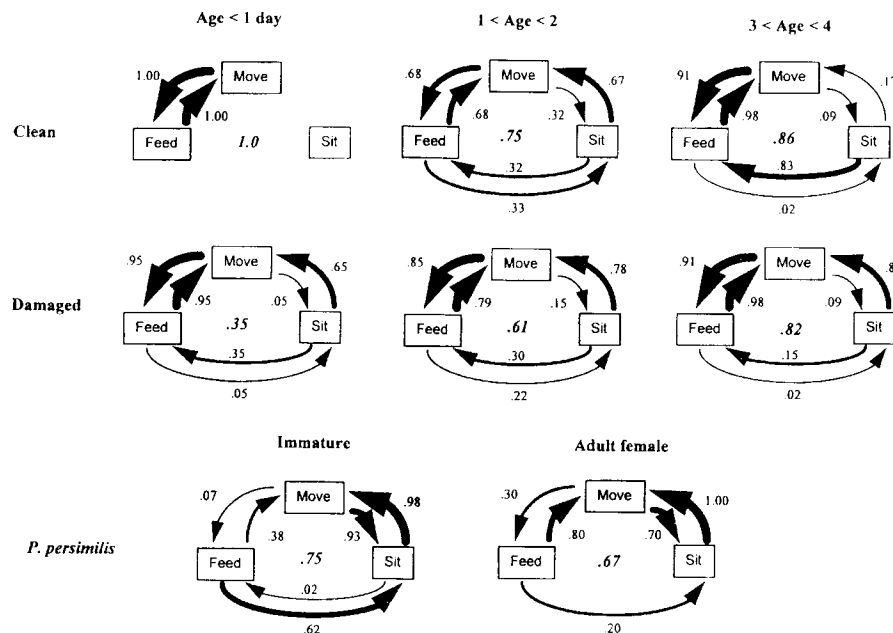


Fig. 6. Flow diagrams of behavioural activities for each treatment group. The numbers associated with an arrow are conditional probabilities of an indicated transition; the widths of the arrows are approximately proportional to the transition probabilities. The bold numbers in the centre of each diagram are the overall stereotypy values for that group.

adults may explain the larger proportion of resting we observed in the juveniles. One may consider the adult females as anabolic egg factories on leaves with abundant *T. urticae*. In the presence of abundant prey, the availability of food is not as limiting as gut absorption and anabolic yolk deposition. Satiation is important in the predator foraging process (Sabelis, 1985). Although, based on handling time, adult female *P. persimilis* could potentially consume 12 prey eggs per hour, they actually consume approximately one egg per hour (Sabelis, 1981). The total feeding times we observed agree with those reported by Eveleigh and Chant (1981b) in their observations of successive feeding events. After feeding, predators engaged in area-restricted searching behaviour (Eveleigh and Chant, 1981b) and reduced the length of moving bouts. Because some adults spent a long time in following the edge of the leaves, there was great variance in the length of movement bouts.

We must temper the extrapolation of our results, based on behaviours for limited times in limited arenas, to the real world. In the natural environment in which these two species interact they can move up the stems of plants to new leaves and even to new plants. Confining the predator in particular may explain

why the predation rate in our study was five times greater than what Sabelis (1981) reported for gravid females. Furthermore, both predators and prey may disperse aerially as well as by walking; this avenue was not available to mites in our test. Nonetheless, the trends we found regarding the spider mite age and leaf damage are consistent with the patterns of movement and feeding found in more natural settings. The predator-prey interaction is dependent upon the local movement of both predators and prey (De Roos *et al.*, 1991); movement plays a key role in locating new food resources. This study of specific movement behaviours is a step towards developing a behaviourally-based understanding of the population dynamics of these two species.

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